

The Distribution of *Woodwardia areolata*

R. CRANFILL*

Phytogeographical studies in North America, as compared with those in Europe, are still in their infancy. Lack of detailed atlases and the relative paucity of extensive paleo- and neocological studies in North America hamper the botanist who wishes to investigate the factors affecting the distribution of a particular species. A few botanical studies of this sort are available (Hocker, 1956; Koevenig, 1976; Salisbury, 1926), although most are limited to local areas or to single factors.

The distribution of a particular plant is determined by several interrelated factors, including: (1) climate and soils, both present and past, (2) interactions with other organisms, (3) production and dissemination of propagules, and (4) evolutionary history, including time and place of origin (Billings, 1952; Cox et al., 1976; Krebs, 1972; Pielou, 1979). In general, physical parameters of the environment, such as moisture availability or extremes of temperature, place absolute limits on the distribution of an organism. Interactions with other species (including man!), soils, dispersability, and other historical factors (e.g., hurricanes, stream piracy, and glaciation) constrain the organism within these bounds (Billings, 1952; Gorham, 1954). As many have pointed out (Cox et al., 1976; Koevenig, 1976), the study of the interaction of limiting factors is problematic because of our inability to deal quantitatively with several seemingly inextricably linked variables at once. Analysis of widespread or narrowly restricted species is often easiest because in these situations one or a small number of variables contributes differentially to the distribution. Even so, the implications of such correlations are not always as clear as they may seem. In the absence of corroborative experimental evidence, caution should always be exercised in the interpretation of distributional correlations.

Woodwardia areolata (L.) Moore is ideal for this type of study because it is widespread and common throughout the southeastern and Atlantic United States and is well collected. One of the three species in subgenus *Lorinseria*, it is characteristic of acidic mucky, sandy, and peaty bogs throughout the southeastern United States (Wherry, 1921, 1964). The aim of this paper is to make some ecological inferences from the distribution of *W. areolata* and to discuss some of the problems inherent in this sort of induction.

MATERIALS AND METHODS

The distribution of *W. areolata* was compiled from herbarium specimens deposited at the following institutions: DHL, F, FLAS, FSU, GH, KY, MEM, MICH, MO, NCU, NY, SMU, TAES, TENN, TEX, TNS, UC, USF, VDB (abbreviations of Holmgren et al., 1981). Over 700 sheets were examined and plotted accurately on a base map of the eastern United States and Canada. Climatic and edaphic parameters were drawn from a variety of sources. Isotherms were composed and redrawn from individual state maps (National Atmospheric and Oceanographic Institute, 1980).

*Department of Botany, University of California, Berkeley, CA 94720.

RESULTS AND DISCUSSION

The distribution of *W. areolata* is shown in *Fig. 1*. A specimen found at USF (*Cheever s. n.*, 25 June 1917) verifies the occurrence of this species in Maine (previously questioned by Ogden et al., 1948). It also seems likely that the species may occur in southern Indiana and extreme eastern Kansas. Associations of the distribution with several edaphic and climatic factors were found and are discussed below.

Climatic Factors.—The climatic feature that appears to have the greatest influence on *W. areolata* is minimum winter temperature. Of the three isotherms examined (0°C, -2.0°C, and -4.5°C), the -4.5°C mean made the closest fit. All stations, save five, fell to the south of the line, with especially close correspondence in New England. Of the sites north of the isotherm, three are no longer extant (Kitfield, 1974; Price, pers. comm.), while another lies close to the Atlantic Ocean which may have a moderating influence not reflected in the climatic data. It is interesting to note the absence of this species from the higher Appalachians of Virginia and West Virginia (Wagner, 1963), even though suitable acidic bogs and seeps exist in the area.

It is apparent that mean temperature in itself is not a very useful index. As an indicator of potential climatic severity it can be important, although analysis is nearly impossible in the absence of values for variance. Thus, survival of *W. areolata* may not depend as much on its tolerance of -4.5°C as on its ability to withstand the occasional much colder winter. Of course the problem may be even more complex. Winter minima may reflect other associated parameters, such as the length of the growing season, that more directly affect the ability of the plant to grow, reproduce, and compete with its neighbors.

Competition can be critical in the distribution of organisms (Hynes, 1954; Jaeger, 1970). Since competition varies as a function of community composition, which changes over the distribution of any particular species, a perfect or even very close fit between abiotic influences and distributional limits often does not obtain. Distributions of weedy species, therefore, probably more closely parallel absolute climatic limits than do distributions of plants of stable habitats, where interactions with other organisms are more structured. The recent northward spread of *Asplenium platyneuron* (L.) B.S.P., primarily a southern species, is a result of an increase in the disturbed habitats that provide this species with suitable sites in which to become established (Wagner and Johnson, 1981) and demonstrates that the previous exclusion of this spleenwort was more a result of its competition with established communities than a result of its tenderness. A similar explanation may account for the presence of *W. areolata* on siliceous cliffs and ledges at the northern and western limits of its range, even though seemingly suitable bogs and seeps exist in these areas. At some point, the species composition of the typical habitat of this species changes sufficiently so that it no longer is competitive in such situations. Sandstone cliffs and ledges in the same vicinity, which present physiological demands similar to those of acidic bogs (in the form of nutrient inavailability and drought stress), possess less plant cover and are characterized by a much lower diversity of species. It seems likely, therefore, that lithophily in *W. areolata* may be a

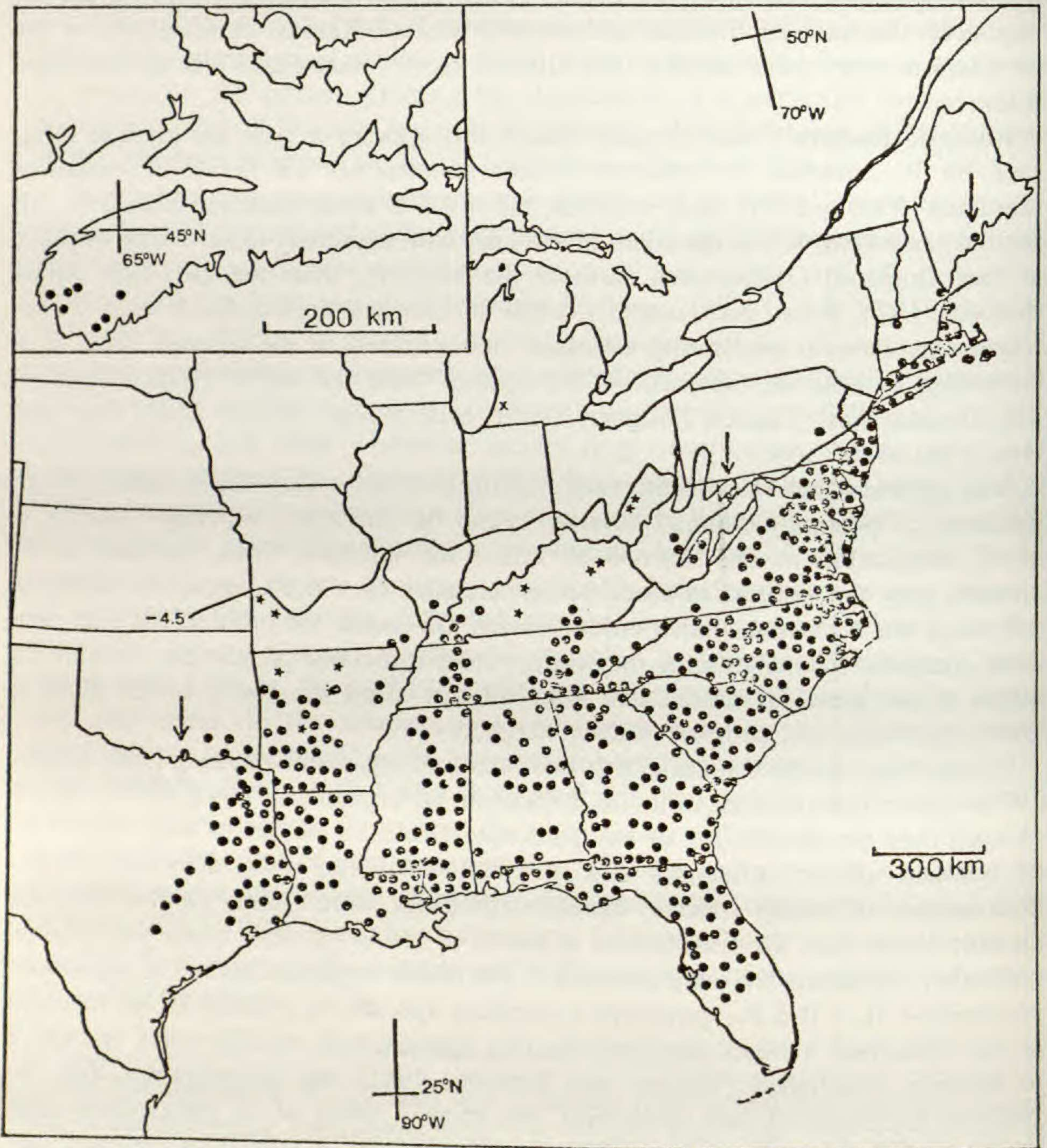


FIG. 1. Distribution of *Woodwardia areolata*. Dots represent terrestrial and unspecified occurrences while stars indicate epipetric stations. The ragged line represents the January -4.5°C isotherm. Inset shows Canadian province of Nova Scotia. X indicates extirpated population. Arrows indicate outlying populations.

direct response to competition. Such cases would be parallel to but more subtle than Billings' (1950, 1952) "Compensation Effect," in which edaphic factors of certain soils and rock types compensated for the negative effects of other environmental factors. Transplants of individuals of *W. areolata* from Kentucky to Michigan survived over two winters (until 1981 when the experiment was discontinued) and indicate that winter minima alone are insufficient to account for the distribution of this fern. Further demographic and transplant experiments are needed to adequately test the hypothesis that competition is the controlling factor.

Edaphic Factors.—The distribution of *W. areolata* fitted that of certain soil types even better than it did temperature. My measurements and those of Wherry (1921) indicate that the sporophyte of this fern is extremely acidophilous. The pH of several sites checked in Kentucky and Tennessee all fell below 5.5, with one reading of 4.0. It is not surprising then that the species is entirely absent from calcareous regions within its range. No stations are known in the limestone regions of the Interior Low Plateaus or in the calcareous Black Belt region of Alabama and Mississippi. Absence of the species from glaciated areas in southern Illinois and southeastern Ohio can be ascribed to the predominance of calcareous glacial drift in these areas (Fig. 2). The alluvial plain of the lower Mississippi River is also avoided. As a region of heavy basic to circumneutral clays (Kellogg, 1936; Braun, 1950), the Mississippi Alluvial Plain is devoid of most species characteristic of the sandy uplands and acidic seeps to the east and west. Correspondence of the distributions of *W. areolata* and *Pinus echinata* Miller (Little, 1971), another calcifuge, is striking.

The best fit to soils occurs in eastern Texas (see inset, Fig. 2). The absence of the Chain Fern from the regions of the Blackland Prairie and Coast Prairie soils, both predominantly calcareous clays (Arbingast et al., 1976), is striking. Because of their greater matrix potential, clay soils must be hydrated to a higher percentage than coarser grained soils to exceed the permanent wilting percentage. As a result, clay soils tend to be droughtier in more arid regions and may become critical for *W. areolata* as it reaches its western limit. The patchwork distribution of these soils has made it impossible, therefore, to assess the relative importance of moisture availability (for an index, see Thornthwaite, 1948) and relative humidity as limiting factors; no good correlation was found between these factors and the western limit of *W. areolata*.

As with the consideration of climate, distributional evidence is insufficient to demonstrate that heavy clay soils or pH are in themselves limiting. The indefinite survival of adult sporophytes on the heavy, calcareous, nutrient-rich soils of the Inner Bluegrass region of Kentucky indicates that competition may actually constitute the limiting factor.

The absence of this fern from much of the Allegheny Plateau cannot be explained by the climatic or edaphic criteria just discussed. Contrary to its name, the plateau region is highly dissected and affords little of the seep and bog habitat necessary for the species. It also lacks extensive deposits of resistant sandstone and conglomerate that form the secondary habitat of the fern.

Although the previous discussion concerned the sporophyte, other stages in the life history may be important in controlling the distribution. Pteridophytes are like

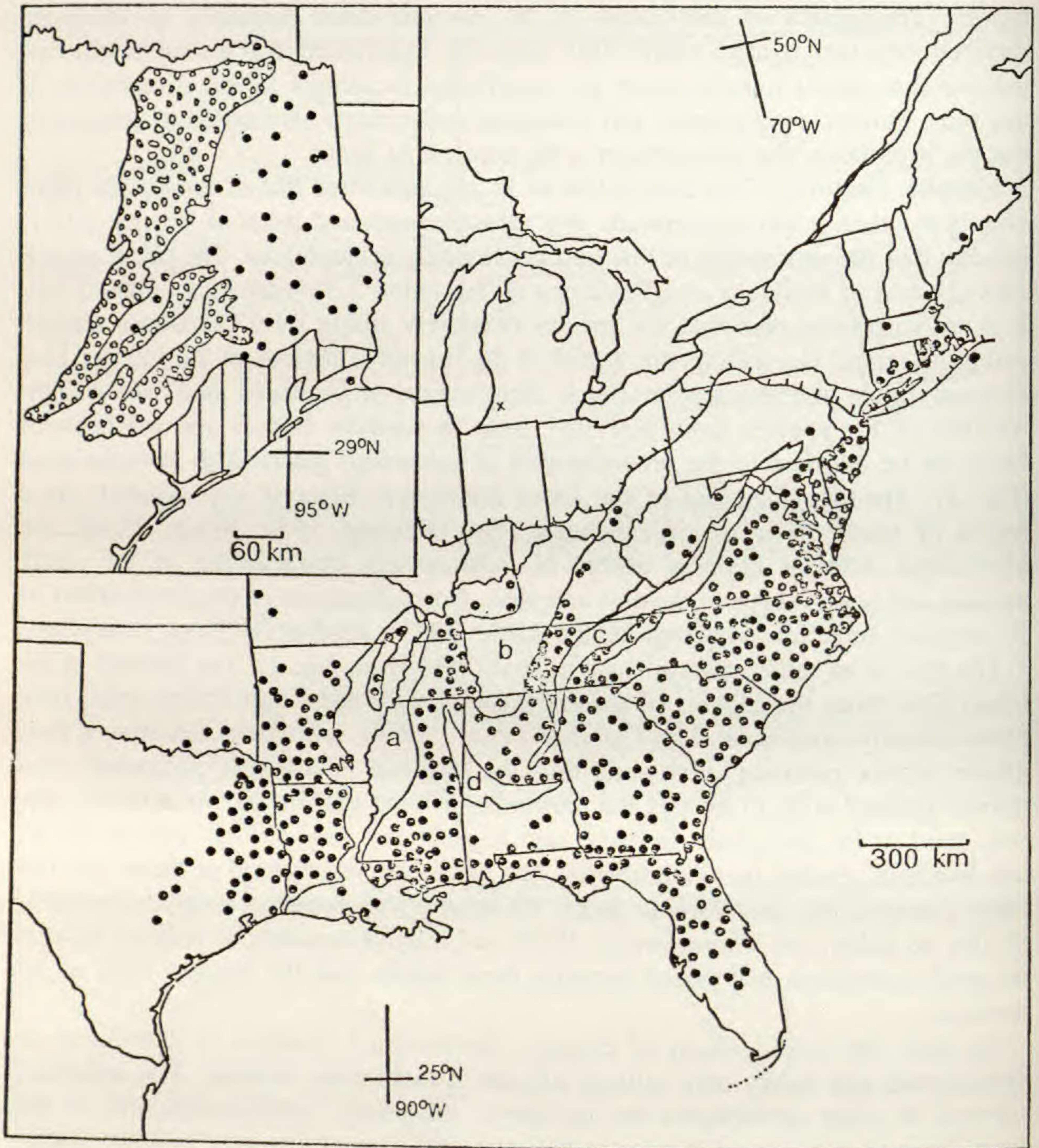


FIG. 2. Distribution of *Woodwardia areolata* in relation to soils; a = Mississippi Alluvial Plain, b = region of Interior Low Plateaus with calcareous soils, c = Ridge and Valley Province, d = Black Belt region. Inset shows enlargement of the distribution in Texas; cobbled area represents the region of blackland prairie soils while crosshatched area represents the extent of coastal prairie soils. Hatched line depicts extent of Wisconsin Glaciation. X indicates extirpated population.

lower plants in which the alternation of generations can have drastic consequences on the distribution of the organism (see the example of *Laminaria*, Dixon, 1965, pp. 109–115).

In summary, the present distribution of *W. areolata* is clearly associated with the mean -4.5°C minimum January temperature to the north. The distribution of calcareous soils, especially clays, effectively limits the distribution to the south and may be important, in concert with increasing aridity, to the west. No correlation was found between the distribution of this fern and the indices of moisture availability and relative humidity. In all cases it appears likely that competition narrows the limits imposed by abiotic influences since preliminary experiments demonstrate the ability of this species to survive in more rigorous environments when competition is removed. The change from bogs and seeps to cliffs and ledges at the range limit is also compatible with this hypothesis. This "competitional compensation point" is probably more important in limiting the distributions of non-weedy species, which occupy more stable habitats than do weedy species.

Experimental studies of problems of distribution are greatly needed. Through narrowing and refining our investigations, they may aid materially in the study of the effects of competition on community structure. Ferns make excellent subjects because they are small and fairly easy to grow and because the production and dissemination of propagules, critical in many flowering plants, is not so limiting in pteridophytes.

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REVIEW

FERNS AND FERN ALLIES OF THE DRIFTLESS AREA OF ILLINOIS, IOWA, MINNESOTA AND WISCONSIN, by James H. Peck. Milwaukee Public Museum Contributions in Biology and Geology 53:1-140. 1982. \$13.50 postpaid. —The driftless area, a pocket in the upper midwestern landscape which escaped at least the more recent glaciations, holds, by virtue of its topography and age of its habitats, a diverse and interesting array of plants. It has been the subject of botanical study for many years. The present account is by far the most complete and useful of any we have had for the pteridophytes, which number 73 species, 13 hybrids, and 6 infraspecific taxa. Peck's treatment includes a useful introduction, a discussion of the affinities of the flora with special reference to the interesting disjunct *Thelypteris simulata*, a systematic list with synonyms, statement of habitat, and specimen citations, a key to the genera and species of pteridophytes found in the driftless area, and a large and useful section of literature cited. Ninety pages are devoted to full-page county distribution maps for the driftless area ferns that include all of Minnesota, Wisconsin, Iowa, Illinois, and Missouri. The maps not only place the ferns of the driftless area in the context of the surrounding region, but they are sure to stimulate searches for pteridophytes in counties where the first records are yet to be obtained.—D.B.L.